








RESEARCH ARTICLE

Direct and indirect effects of invasive species: Biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning

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Funding information

Schweizerischer Nationalfonds zur
Förderung der Wissenschaftlichen
Forschung, Grant/Award Number:
400440_152085; Swiss Agency for
Development and Cooperation; CABI

Handling Editor: Peter Alpert

Abstract

1. Global change, such as exotic invasions, dramatically affects ecosystem functioning. However, the mechanisms behind the impacts are often unclear and despite extensive experimental work, we know little about the importance of biodiversity loss as a component of global change effects in real-world ecosystems.
2. We disentangled several mechanisms by which an exotic invader affected ecosystem functioning in East African drylands in Kenya and Ethiopia. We used structural equation modelling to separate direct effects of a woody invader *Prosopis juliflora* on a range of ecosystem functions from indirect effects mediated through changes in biodiversity (plant species richness) and ecosystem functioning (herbaceous biomass). We analysed effects on ecosystem functions linked to soil biogeochemical cycling and transfer of energy between trophic levels.
3. We found that the mean size of individual indirect effects mediated by biodiversity and herbaceous biomass was about twice as large as the mean size of individual direct effects of *Prosopis* on ecosystem functions, showing that indirect effects are an important component of the invader's overall environmental impacts. Changes in both herbaceous biomass and biodiversity were approximately equally important as drivers of indirect effects, indicating that we need to expand our view of indirect effects to consider a wider range of mechanisms. Simple univariate models failed to capture some *Prosopis* invader effects because positive direct effects on soil stability and predatory invertebrates were counteracted by negative indirect effects on biodiversity or biomass loss. The majority of effects were similar in both study systems. Suggestions that woody invaders are able to

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increase certain ecosystem functions may therefore have arisen because these negative indirect effects were not considered.

4. *Synthesis.* Our study indicates that successful management of exotic invasions is likely to require not only control of the invader but also restoration of diverse and productive herbaceous communities as they are important for many ecosystem functions. This highlights the importance of biodiversity as a driver of ecosystem functioning also in real-world systems.

KEYWORDS

Drylands, global change ecology, invasion ecology, *Prosopis*, structural equation model

1 | INTRODUCTION

Ecosystems are threatened by global change drivers including land-use change, invasive species and climate change, all of which are altering biodiversity and the functioning of ecosystems (Sala et al., 2000). To better predict and manage global change, it is critical to understand the mechanisms by which global change drivers affect ecosystem functioning and in particular to understand if biodiversity loss is an important component of global change effects (Allan et al., 2015). Experiments have shown that diverse communities generally have higher ecosystem functioning than less diverse ones, suggesting that a loss of biodiversity will reduce functioning (Cardinale et al., 2012). However, it is only recently that studies have shown that biodiversity loss in 'real-world', natural or managed ecosystems, can have a strong effect on functioning (e.g. Delgado-Baquerizo et al., 2015). Therefore, to understand the importance of biodiversity loss, we need to compare the effects of biodiversity change with other drivers of ecosystem functioning, in ecosystems altered by global change drivers (Giling et al., 2018).

Invasive species are major global change drivers (Pejchar & Mooney, 2009) and many studies have shown that they can alter biodiversity (e.g. Vilà et al., 2011) and ecosystem functioning (e.g. Pejchar & Mooney, 2009). However, most have looked at effects of invaders on single functions (van Wilgen & Richardson, 2014) and in single environmental contexts (Dassonville et al., 2008) and only one study (Constán-Nava, Soliveres, Torices, Serra, & Bonet, 2015) has tried to quantify the functional importance of biodiversity-mediated, indirect effects. Direct effects of invaders on ecosystem functioning could arise through alterations in disturbance regimes or nutrient levels. Indirect effects of biodiversity loss will only be important in comparison if invaders strongly reduce biodiversity and if biodiversity strongly affects functioning. Studies of other global change drivers have found variation in the importance of direct and biodiversity-mediated indirect effects: Allan et al. (2015) showed that indirect effects of land-use intensification on ecosystem functioning, mediated by plant diversity, could be just as strong as the direct effects, while a study by Isbell et al. (2013) showed that indirect effects of diversity loss occurred but were much smaller than direct effects of nitrogen addition. However, so far, only a handful of studies have quantified the functional importance of biodiversity loss in

a global change context and we need to integrate studies on invasions with biodiversity-functioning research to better understand the importance of biodiversity loss as a driver of invader effects on ecosystem functioning.

Many experiments have shown that a loss of plant diversity can reduce the ecosystem function of biomass production (e.g. Hector & Bagchi, 2007). These diversity-induced changes in biomass may have consequences for other ecosystem functions, as high rates of plant biomass production may be linked to high abundance and diversity of insects (Borer, Seabloom, & Tilman, 2012) or may increase soil carbon (Lange et al., 2015). The effects of plant diversity on a range of functions may, therefore, be mediated by changes in plant biomass production. In addition, plant biomass is likely to be directly affected by invasive plant species, which can either increase (Maron et al., 2014) or reduce plant biomass (Ndhlovu, Milton, & Esler, 2011). Invasive species might therefore affect ecosystem functioning indirectly through changes in plant diversity, plant biomass or both, i.e. a loss of plant diversity reduces biomass production and other functions in turn. We can therefore distinguish between three indirect effects of invaders on functioning: those mediated through only diversity, only biomass or through both richness and biomass. However, very few studies have considered how invader and biodiversity effects might propagate through the ecosystem to affect related functions and we therefore do not know how important changes in biomass and diversity are as indirect effects of invaders.

It is often challenging to determine if invasive species are really the drivers of environmental change or are merely passengers. For instance, disturbance may increase invasion and may also affect ecosystem functioning (Didham, Tylianakis, Hutchison, Ewers, & Gemmell, 2005). Evidence for both the passenger (Macdougall & Turkington, 2005) and the driver model (White et al., 2013) has been found in different systems. Yet, understanding whether invasive species are drivers or passengers is crucial for developing sustainable management (White et al., 2013). Structural equation modelling (SEM) techniques can be used to test the combined effects of disturbance and invasive species on ecosystem functioning in order to resolve this question (e.g. Pagnucco & Ricciardi, 2015). To our knowledge this has not been done for woody species.

In order to determine the importance of biodiversity loss as a component of invader impacts, we tested the mechanisms by which



FIGURE 1 Landscapes with low *Prosopis* cover in Ethiopia (top-left) and Kenya (lower-left) compared to high *Prosopis* cover levels in Ethiopia (right) [Colour figure can be viewed at wileyonlinelibrary.com]

Prosopis juliflora (Sw.) DC (*Prosopis* henceforth), an alien invasive tree, influences ecosystem functioning in two Eastern African dry-land areas. Specifically, we aimed to assess: (a) which functions were affected by *Prosopis*, (b) whether these effects of *Prosopis* were direct or were mediated by biodiversity loss and/or biomass change, (c) whether results were consistent between regions and (d) whether *Prosopis* is a driver of change or merely a passenger.

2 | MATERIALS AND METHODS

2.1 | Study sites

The effects of *Prosopis* on biodiversity and ecosystem functioning were studied in two Eastern African regions: Baringo County, Kenya, and Afar Region, Ethiopia. *Prosopis* was introduced to Eastern Africa in the 1970s and 1980s and has since become invasive. Many invasive trees have caused substantial problems in Africa but this region, except for South Africa, remains severely understudied (Pyšek et al., 2008). This is especially problematic given that many livelihoods in Africa directly depend on functional ecosystems and people are therefore vulnerable to the effects of invasive species (Witt, 2010). *Prosopis* was introduced to drylands worldwide in the second half of the 20th century to improve livelihoods by increasing soil fertility and soil stability and providing wood (Shackleton, Le Maitre, Pasiecznik, & Richardson, 2014). Since then, *Prosopis* has become problematic worldwide, as it reduces biodiversity and herbaceous biomass (Shackleton, Le Maitre, Van Wilgen, & Richardson, 2015), hosts mosquitoes (Mueller et al., 2017) and lowers the ground water table (Dzikiti et al., 2013). However, quantitative data on *Prosopis*'s

effects on ecosystems remain rare and most studies have only looked at single functions. Baringo and Afar were among the first regions to be invaded by *Prosopis* in Eastern Africa and have high variation in cover levels. In Baringo, data were collected in the area around Lake Baringo and Lake Bogoria (between 0°13' and 1°40'N and 35°36' and 36°30'E). Baringo has a semi-arid climate, with a yearly average temperature of 24.6°C and annual rainfall of 635 mm (Kassilly, 2002). Afar region is also located in the Great Rift Valley (between 8°49' and 14°30'N and between 39°34' and 40°28'E), and has a semi-arid climate similar to that in Baringo, with an annual average temperatures of 27.6°C and 564 mm of annual rainfall (Werer Agricultural Station, 2000). Prior to invasion, the vegetation in Afar and Baringo consisted of a mix between mainly degraded grassland, wooded grassland and shrubland (Kiage, Liu, Walker, Lam, & Huh, 2007; Shiferaw et al., 2019). The level of grassland degradation at the time of *Prosopis* invasion differed between the two regions (Figure 1); while in Baringo many of the grasslands were already degraded in the 1970s, degradation of grasslands in Afar was particularly prominent in the decades after the introduction of *Prosopis*. For example, since 1986 some 25% of the perennial grasslands have changed to annual grasslands or to barren land (Shiferaw et al., 2019). Our sampling mainly took place in degraded grasslands and native woody species were mostly absent from our plots.

2.2 | Plot selection

Sampling was performed in ten rural communities per region (Supporting Information S1), defined as the smallest administrative unit, kebele in Ethiopia and sublocation in Kenya. Communities

were selected to differ in their overall level of invasion, so that they formed a gradient in *Prosopis* cover which ranged from 4% to 69% at the community level. Communities were selected purposely to be close to each other to minimize climatic variation but have a maximum range of *Prosopis* cover. Within each community, five to eight 15 × 15 m plots were established and marked with a GPS, again along a *Prosopis* cover gradient. All plots within a community were selected to have a similar land-use history but land-use history could differ between the communities. Sampling took place during the rainy seasons of 2015 and 2016 in Ethiopia and 2016 and 2017 in Kenya.

2.3 | Biodiversity and ecosystem functioning measures

Herbaceous biomass and plant species richness were measured in the plots. Each plot was divided into nine 5 × 5 m² subplots and only the four corner subplots and the central subplot were sampled. Four of these five subplots were randomly selected and the abundances of all plant species were assessed in 1 × 1 m² quadrats located in the centre of the subplots. When setting up the plots 6–12 months before sampling, we fenced off one of the five subplots with barbed wire to estimate biomass without grazing. However, most fencing was destroyed, so we ended up not using these subplots. Nevertheless, even with only four subplots, we provide a good estimate of the plot level soil and vegetation characteristics. A 1 × 1 m² frame, divided into one hundred 10 × 10 cm², was placed over each quadrat and cover was measured by counting the number of squares occupied by each species. Since cover within an occupied 10 × 10 cm² could be less than 100%, this method likely overestimated cover. However, canopies of *Prosopis* were large in comparison to squares and cover within a canopy was generally close to 100%. All additional plant species present in the whole plot were also recorded. Within the 25 × 50 cm² centre of each 1 × 1 m² quadrat, all above-ground biomass was cut and oven-dried to determine dry weight. In Kenya, only 33 herbaceous biomass samples were available for plots on which soil and invertebrate measures had also been taken. However, log-transformed plant cover and log-transformed herbaceous biomass were significantly related ($p < .0001$; $r^2 = .54$), so we used log-transformed plant cover as a proxy for herbaceous biomass in Kenya. For consistency, herbaceous biomass was also log-transformed in Ethiopia.

In the same four subplots in which vegetation was recorded, two one meter transects were laid out to assess soil stability using the qualitative scoring system developed by Tongway and Hindley (2004). In brief, litter, cryptogam cover, crust brokenness, erosion type, deposited materials, surface roughness and surface nature were scored qualitatively. To measure soil nutrients, in the same four subplots, we took eight soil cores, to 15 cm depth, at haphazard locations and pooled them. Soil samples were subsequently analysed at Haramaya University (for Ethiopia) and the Kenyan Agricultural and Livestock Research Organization, Nairobi, (for Kenya). Available phosphorus was analysed with NaHCO₃ extraction (Watanabe & Olsen 1965). Total nitrogen was analysed using the Kjeldahl method

(Kjeldahl, 1883), not all of the soil nitrogen is available for plants but total soil nitrogen was taken to indicate the overall fertility level. Soil organic carbon (SOC) was measured using wet oxidation (Walkley & Black 1934) and pH was determined using a 1:2.5 soil–H₂O solution (MC Lean, 1982). Soil texture was measured using a hydrometer and divided into percentages of sand, silt and clay (Bouyoucos, 1962). The cation exchange capacity (CEC) was determined using ammonium acetate (Metson, 1957). Additionally, three bulk density cores were taken in the centre of each plot; cores were then dried and the weights averaged. Bulk density was used to convert the nitrogen, SOC and phosphorus concentrations to stocks (kg/plot), however CEC was not converted and is expressed as a percentage. Reference samples were sent to each laboratory, which showed that absolute values differed between laboratories, but the relative differences between samples were similar. In order to remove differences between laboratories, we fitted linear models with soil properties as response variables and region (lab) as explanatory variable and extracted residuals.

Wild pollinator, excluding *Apis mellifera* L., and parasitoid wasp abundance were sampled using pan traps (Westphal et al., 2008). One pan trap was placed in the middle of a plot for one week. Each trap consisted of three bowls, painted in UV-bright white, blue and yellow respectively, and filled with 50% ethylene glycol and 50% water. Mosquitoes were trapped using BG-sentinel 2 traps (Biogents) baited with two odours as the attraction mechanism. a combination of mbita blend to simulate human skin odour (Mukabana et al., 2012) and a yeast, sugar and water to release CO₂ (Smallegange et al., 2010) were used to replicate human skin emanations and human breath respectively. Mosquito traps were put in the field for two nights per plot and operated between 18:00 and 06:00. Pan traps and mosquito traps were put out on the same night on all plots within a community but were put out on different nights in different communities. Pollinators, parasitoids and mosquitoes were not sampled in Ethiopia for logistical reasons. We also sampled invertebrates by beating the vegetation: we sampled the ground layer and woody layer separately, in the centre of each vegetation subplot. In each case, the vegetation was beaten eight times and all invertebrates were collected on a 1 × 1 m² white cloth spread underneath the vegetation. Invertebrates were stored in 70% alcohol and identified to order, morphospecies within order and to the trophic level (herbivore or predator). Ants were removed from the analysis because their abundance was highly variable between plots.

2.4 | Statistical analysis

All analyses were performed in R version 3.4 (R Core Team, 2018). First we tested the effect of *Prosopis* on individual biodiversity and ecosystem functioning variables, using linear mixed models, fitted with the package nlme (Pinheiro et al., 2018). We were not interested in modelling absolute ecosystem function values, or in testing for differences between regions, but rather in assessing effects of *Prosopis* on ecosystem functions. Therefore, we took residuals of a regression of each individual function against region, to compare *Prosopis*

effects. This allowed us to show the average effect of *Prosopis* across the two regions (the slope, or different slopes if the interaction was significant) while ignoring variation in overall ecosystem functioning between regions (intercepts). In all models, community was used as a random variable, as land-use history could differ between communities. We took residuals to correct for potential differences due to elevation, pH or soil texture (we used residuals rather than fitting multiple regressions to make these models comparable with the SEMs, see below).

Second, to assess how *Prosopis* directly and indirectly affected ecosystem functioning, we fitted SEMs using the package *LAVAN* (Rosseel, 2012). In addition to including the direct effect of *Prosopis* on all ecosystem functions, we also included indirect effects, which could be mediated via plant species richness and/or herbaceous biomass. Plant species richness was included as many experimental studies have shown effects of biodiversity on all the functions considered here (Cardinale et al., 2012). Herbaceous biomass was included because experimental studies have shown that it can influence both invertebrate (Borer et al., 2012) and soil measures (Lange et al., 2015). We also included a link between biodiversity and herbaceous biomass, which has been shown in many experiments (Cardinale et al., 2007), to test whether indirect effects of biodiversity on functioning were mediated by changes in biomass production.

We also included an effect of disturbance on all variables in the SEMs to test whether *Prosopis* was a driver or passenger of change and to test for direct effects of disturbance on ecosystem functions. The disturbance index consisted of three measures closely linked to disturbance in drylands: the human population density in each community and the livestock density (Dregne, 2002), expressed in dry sheep equivalents (Muir & Simpson, 1987) and the distance from each plot to the nearest village (Shackleton, Griffin, Banks, Mavrandonis, & Shackleton, 1994). These three measures were standardized between 0 and 1 individually and summed as an indicator for disturbance. A conceptual model of our analyses is shown in Figure 2.

As sample size was limited, separate SEMs were created to test the effect of *Prosopis* on herbivorous and predatory invertebrates, pollinators, parasitoids, mosquitoes and soil variables. Herbivorous and predatory invertebrates were analysed in one SEM to test for possible cascading effects (Scherber et al., 2010). We hypothesized that the vegetation would influence the soil variables (Constán-Nava et al., 2015), however, soil nutrients can also affect the vegetation (e.g. Crawley et al., 2005). We therefore tested SEMs in which individual arrows from vegetation to soil variables were reversed. These alternative models always had higher AIC values and we therefore present models with effects of vegetation on soils. We hypothesized that *Prosopis* would decrease plant species richness and herbaceous biomass. Invasion success can, however, be lower in diverse plant communities (Bennett et al., 2016) and tree establishment can be hindered when competition with herbaceous species is high (Morrison, Holdo, Rugemalila, Nzunda, & Anderson, 2019). We thus tested alternative models with the arrows from *Prosopis* cover

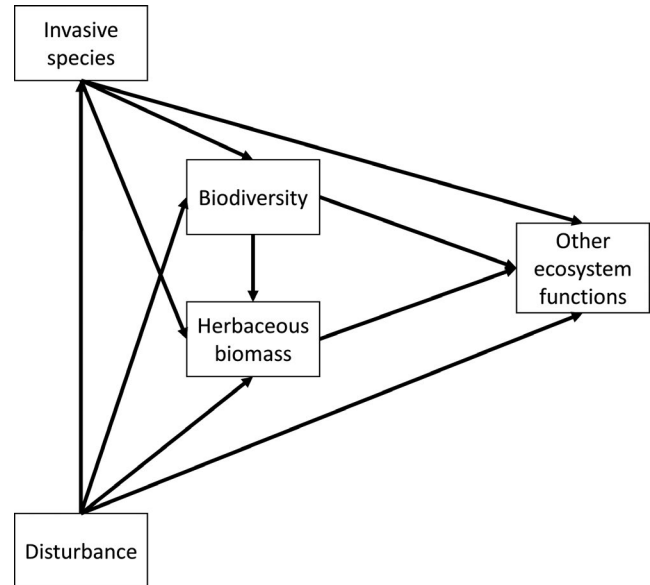


FIGURE 2 Conceptual model of tested relationships to assess whether *Prosopis* effects on ecosystem functioning are direct or mediated by vegetation, as well as the role of disturbance on *Prosopis* effects

to plant species richness and herbaceous biomass reversed. These alternative models always had higher AIC values and were therefore not used further in the analysis. An overview of the paths initially tested in each model can be found in Supporting Information S4.

To correct for potential correlations with environmental factors, all variables that were used in the SEM were first corrected for potential differences due to pH, soil texture and elevation by taking residuals (Soliveres et al., 2016). For mosquitoes, we additionally took residuals for the distance to the nearest water body and village and, for pollinators and parasitoids, for the distance to the nearest crop field.

We used multigroup SEMs to compare both regions. We tested whether each path differed between regions by comparing a model with each individual path either constrained to be the same in the two regions or unconstrained. In each case, the model with the lowest AIC was chosen, however, if the AIC difference was <2 (Burnham & Anderson, 2004), we used the simpler, constrained model. As we had a relatively low sample size for some models, we simplified full models (Supporting Information S4). Simplification was done by stepwise removal of the least significant paths and the model fit was compared using AIC and the chi-square tests. We used bootstrapped standard errors and p-values to assess the strength and significance of each path. All path coefficients were standardized between -1 and 1 and are therefore comparable across paths and models. Direct effects are the path coefficients from *Prosopis* to a given function, while indirect effects were calculated as the product of the effect of *Prosopis* on diversity (or biomass) and the effect of diversity (or biomass) on a given function, i.e. by multiplying both path coefficients. The mean direct and indirect effect of *Prosopis* on ecosystem functioning was derived by calculating the total direct

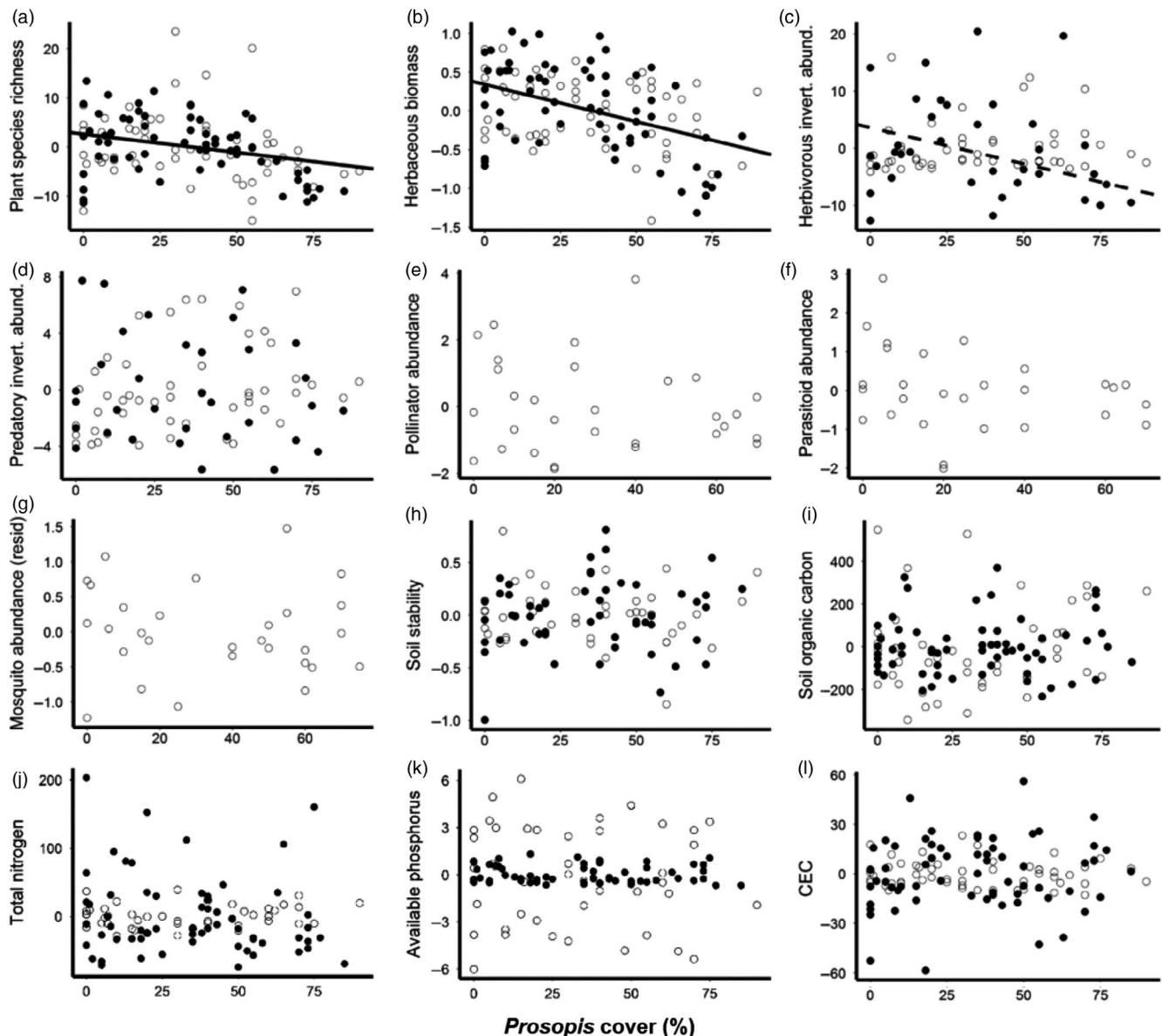


FIGURE 3 The relationship between *Prosopis* cover and multiple biodiversity and ecosystem function indicators, showing residuals after correcting for differences between region. Trend lines are only shown for significant relationships (linear regression: $p < .05$). (a) plant species richness, (b) herbaceous biomass, (c) herbivorous invertebrate abundance, (d) predatory invertebrate abundance (e) pollinator abundance, (f) parasitoid abundance, (g) mosquito abundance, (h) soil stability, (i) total organic carbon, (j) total nitrogen, (k) available phosphorus and (l) CEC. (closed circles = Ethiopia, open circles and dashed line = Kenya, solid line = both regions combined)

and indirect effect for each function separately and then averaging these totals. For direct effects that were calculated in multiple models (*Prosopis* → plant species richness and *Prosopis* → Herbaceous biomass), we used the model that had the highest sample size.

As we used a stratified sampling approach, with plots in multiple communities, we also tested whether correcting for community differences significantly affected results. Using *lavaan.survey*, we ran SEMs which were corrected for community. These SEMs showed similar results and six regressions even went from near significant p -values to significant p -values; as these models were more complex and we dealt with relatively low sample sizes, we used the original models without community. This shows our models are robust

to potential spatial autocorrelation caused by the nested sampling design.

3 | RESULTS

3.1 | *Prosopis* effect on single variables

An increase in *Prosopis* cover significantly decreased plant species richness (Figure 3a; Supporting Information S2) and herbaceous biomass (Figure 3b) in both regions. Herbivorous invertebrate abundance also declined in Ethiopia, but not in Kenya, with increasing *Prosopis* cover (Figure 3c). In the simple linear models, *Prosopis* did not significantly

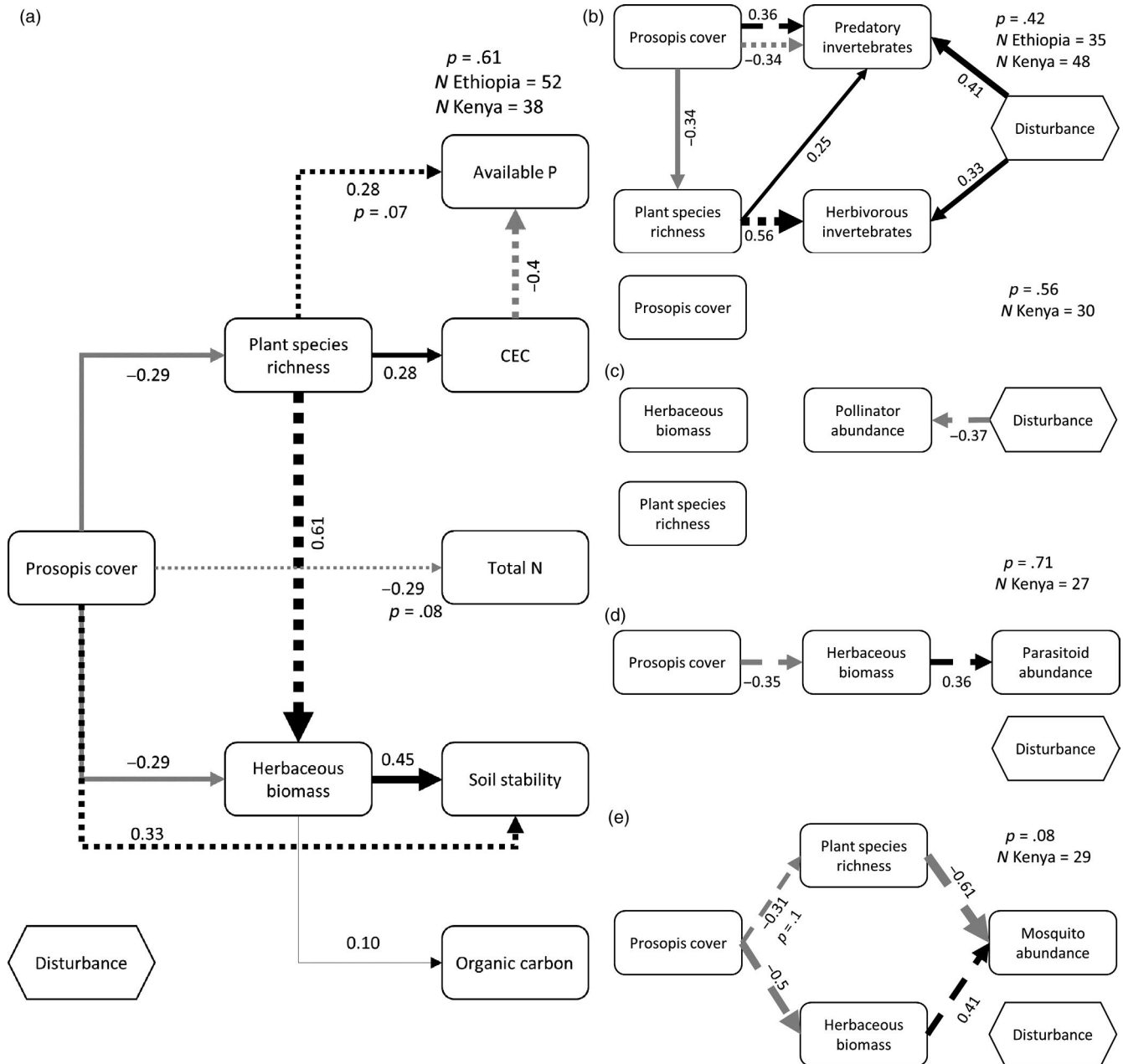


FIGURE 4 Overview of structural equation models: (a) soil, (b) trophic cascade: herbivorous and predatory invertebrates (c) pollinators, (d) parasitoids, (e) mosquitoes. Black lines indicate positive relationships, grey lines negative relationships. Line thickness indicates the strength of the path coefficients. Solid lines = both regions combined, Ethiopia = dotted lines, Kenya = dashed lines. Only significant relationships are shown ($p < .05$), unless indicated otherwise ($p = .05-.1$). N indicates samples available per region, p -value above value of N indicates overall SEM fit (chi-square test)

affect predatory invertebrate abundance (Figure 3d), pollinator- (Figure 3e), parasitoid- (Figure 3f) or mosquito abundance (Figure 3g), soil stability (Figure 3h), SOC (Figure 3i), total nitrogen (Figure 3j), available phosphorus (Figure 3k) or CEC (Figure 3l) in either region.

3.2 | Direct and biodiversity mediated effects of *Prosopis*

Using SEM, we found that *Prosopis* directly increased soil stability in Ethiopia, but not in Kenya, and did not directly influence SOC, CEC

total nitrogen or available phosphorus in either region (Figure 4a; Supporting Information S3). Additionally, *Prosopis* directly reduced predatory invertebrate abundance in Ethiopia but increased it in Kenya (Figure 4b). However, *Prosopis* did not directly affect the abundance of herbivorous invertebrates (Figure 4b), pollinators (Figure 4c), parasitoids (Figure 4d) or mosquitoes (Figure 4e).

Prosopis reduced plant species richness and herbaceous biomass (Figure 4a) and this indirectly reduced a range of ecosystem functions in both regions. These indirect effects are a product of two paths, e.g. the path coefficient from *Prosopis* cover to herbaceous

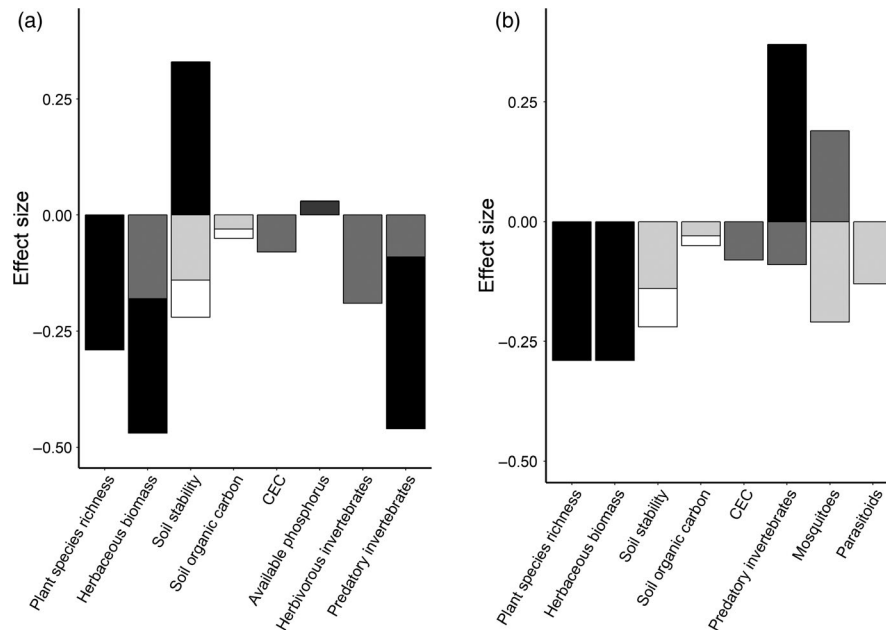


FIGURE 5 Standardized direct and indirect *Prosopis* effect sizes on ecosystem functions in Ethiopia (a) and Kenya (b): direct effects (black), indirect *Prosopis* effects via plant species richness (*Prosopis* → plant species richness × plant species richness → ecosystem function; medium grey), indirect *Prosopis* effects via plant species richness and herbaceous biomass (*Prosopis* → plant species richness × plant species richness → herbaceous biomass × herbaceous biomass → ecosystem function; white), indirect *Prosopis* effects via herbaceous biomass only (*Prosopis* → herbaceous biomass × herbaceous biomass → ecosystem function; light grey) and via CEC (*Prosopis* → CEC × CEC → ecosystem function; dark grey))

biomass multiplied by the path coefficient from herbaceous biomass to soil stability. In total, if we take the means of the coefficients of all the direct and all the indirect effects, indirect effects were stronger than the direct effects, with a mean average standardized effect size of 0.14 compared to 0.06 for direct *Prosopis* effects (Figure 5). We also distinguished three types of indirect effects of *Prosopis*: those mediated by changes in richness alone (mean path coefficient of 0.07), those mediated by changes in biomass alone (0.06) and those mediated by changes in richness and biomass (0.01).

Prosopis had indirect negative effects on both soil stability and SOC in both regions by decreasing herbaceous biomass (Figure 4a). In Ethiopia, *Prosopis* also indirectly reduced herbaceous biomass, via reducing plant species richness, and therefore had further indirect effects on SOC and stability via both plant species richness and biomass. *Prosopis* had an indirect negative effect on CEC by reducing plant species richness in both regions. *Prosopis* therefore indirectly reduced available phosphorus by reducing plant species richness and CEC. *Prosopis* had no significant direct or indirect effects on total soil N (Figure 4a). In both regions, *Prosopis* had an indirect negative effect on predatory invertebrates, via reducing plant species richness (Figure 4b). In Ethiopia, *Prosopis* also indirectly reduced herbivorous insect abundance via reducing plant species richness (Figure 4b) and in Kenya *Prosopis* indirectly reduced parasitoid abundance by reducing herbaceous biomass (Figure 4d). In Kenya, mosquito abundance declined significantly with plant species richness and *Prosopis* had an indirect positive effect on mosquitoes through decreasing herbaceous biomass. However, it also had an indirect negative effect

on mosquitoes via reducing plant species richness (Figure 4e). In the pollinator SEM, *Prosopis* did not significantly affect plant species richness or biomass and so did not have indirect effects on pollinator abundance (Figure 4c). However, the lack of *Prosopis* effects on the plants is possibly due to low power in the pollinator model, compared to the soil and trophic cascade models.

We did not find any specific plant group that reacted particularly strongly to a change in *Prosopis* cover (Supporting Information S5).

3.3 | Disturbance effects

Prosopis cover was not related to disturbance ($p = .23$), but disturbance affected several ecosystem functions related to invertebrates (Figure 4). The mean effect size of disturbance on all invertebrate measurements was similar to the total effects of *Prosopis* (0.22 vs. 0.21). Pollinator abundance was reduced by disturbance, independent of *Prosopis* (Figure 4c). Herbivorous and predatory insect abundance increased with higher disturbance, regardless of *Prosopis* (Figure 4b).

4 | DISCUSSION

Our results show that indirect effects, mediated through loss of plant diversity and/or herbaceous biomass, are a major mechanism by which an exotic invader affects ecosystem functioning. The mean of the coefficients of the direct effects in the various models

was only half as large as the mean of the indirect effects. This also demonstrates that using simple correlational approaches may mask invader effects: *Prosopis* only affected plant species richness, herbaceous biomass and, in Ethiopia, herbivorous invertebrates in simple regression models but had significant effects on all but two functions (soil N and pollinator abundance) in the SEMs. Opposing direct and indirect effects often led to no overall impact of *Prosopis*, such as for mosquitoes, demonstrating that bivariate correlations cannot adequately describe complex ecological relations (Grace et al., 2016). Changes in biodiversity were an important driver of functioning however, some effects on functions were partly mediated by changes in biomass production, showing that indirect effects can occur through multiple mechanisms.

4.1 | Direct and indirect *Prosopis* effects

Prosopis invasion affected many key functions by reducing plant diversity. Many studies have looked at how global change directly and indirectly affects biodiversity (Adler, Dalgleish, & Ellner, 2012; Alexander, Diez, & Levine, 2015), however, few studies have looked at direct and biodiversity mediated indirect effects of global change on ecosystem functions. Testing for the strength of indirect, biodiversity mediated effects, relative to direct effects of global change, is essential to determine if the biodiversity effects seen in experiments (Cardinale 2012) translate to real-world systems. Some studies have found large indirect effects of biodiversity (Allan et al., 2015), whereas others have shown smaller indirect effects of diversity (Isbell et al., 2013) or composition (Manning et al., 2006). In our case, indirect effects, mediated by changes in plant species richness alone, were as strong as direct effects and several effects of *Prosopis* were entirely indirect. We also found that diversity loss offset some positive effects of *Prosopis* on ecosystem functioning: although *Prosopis* directly increased predatory invertebrates this was offset by a reduction in invertebrate abundance following diversity loss. This supports earlier findings that negative indirect effects via loss of biodiversity offset positive direct of *Ailanthus altissima* on soil parameters (Constán-Nava et al., 2015).

In addition to diversity loss, indirect effects could be mediated through changes in biomass. Plant diversity loss reduced herbaceous biomass production in Ethiopia and this reduction in herbaceous biomass reduced soil stability and SOC content. Experiments have also shown that an increase in biomass drives many of the effects of plant diversity on soil carbon (Lange et al., 2015). Woody plant invasions can have mixed effects on soil organic carbon (Jackson, Banner, Jobbágy, Pockman, & Wall, 2002), but our results suggest they are only likely to increase soil carbon if they do not reduce herbaceous biomass. One study showed that *Prosopis glandulosa* can increase soil carbon (Throop & Archer, 2008), however, *P. glandulosa* is deciduous (*P. juliflora* is evergreen in our study area) and might therefore have different effects on biogeochemical cycling. Plant diversity did not increase biomass in Kenya, most likely because overgrazing had resulted in many plant communities with relatively high diversity but low biomass. *Prosopis* also affected biomass directly and this was an

additional pathway by which *Prosopis* indirectly reduced SOC and soil stability. *Prosopis* only indirectly affected parasitoids by changing biomass, perhaps because this reduced vegetation structural complexity. Interestingly, we found contrasting effects of plant species richness and biomass on mosquito abundance. Increased biomass might increase structural complexity and shade, which mosquitoes require for resting (Stone, Witt, Walsh, Foster, & Murphy, 2018), while high plant species richness might reduce mosquitoes by increasing natural enemies or reducing the abundance of favoured plant species (Keesing et al., 2010). The lack of direct effects of *Prosopis* on mosquitoes may be surprising as *Prosopis* can provide nectar (Muller et al., 2017), however, it was not flowering during sampling. Our results show that indirect effects can be complex and mediated through several, sometimes opposing, changes to the ecosystem. Future biodiversity and global change research should therefore consider a wider range of indirect effects on ecosystem functioning.

The majority of effects on soil were consistent between regions but effects on invertebrate abundance were context dependent. *Prosopis* reduced invertebrate abundance in Ethiopia but had no effect on herbivorous invertebrates and actually increased predatory invertebrates in Kenya. These contrasting effects might be explained by differential impacts of *Prosopis* on habitat complexity. Invertebrate abundance can be promoted by habitat complexity (Langellotto & Denno, 2004) and given that Baringo, Kenya, is highly disturbed, *Prosopis* might have increased habitat complexity. In Ethiopia, invasion replaces grasslands with scattered trees by *Prosopis* monocultures, leading to a reduction in habitat complexity. Our findings therefore support previous results showing context-dependency in biodiversity and global change effects due to regional variation in climate (Ratcliffe et al., 2017) or soil fertility (Allan et al., 2015) and suggest that context-dependency in invader effects can be driven by past disturbance. Future studies using a larger selection of sites with differing disturbance levels would however be needed to verify these findings.

4.2 | *Prosopis*—driver or passenger?

Prosopis was likely a driver of change in our study region because its effects on functioning were independent of our disturbance measures. Land degradation by humans and overgrazing are the most important disturbances in our study regions (Mbaabu et al., 2019); our disturbance index quantifies these two effects. In addition, *Prosopis* seeds are often spread by livestock (Van Klinken & Pichancourt, 2015). Disturbances such as droughts or other extreme climate events could also affect *Prosopis* and our ecosystem functions, however, without temporal data we could not evaluate the effects of these events. We therefore cannot be sure we have captured all possible disturbances that might affect *Prosopis*. Invasive species that are drivers of change are typically competitive and capable of dramatically altering ecosystems (Bennett, Thomsen, & Strauss, 2011), like *Prosopis* (Shackleton et al., 2014). Although *Prosopis* seedling survival is reduced by below-ground

competition from native vegetation, it is able to colonize healthy grasslands (Brown & Archer, 1989; Jurena & Archer, 2003). It is therefore not surprising that our study showed *Prosopis* effects to be likely independent of disturbance.

We used structural equation modelling to infer the mechanisms by which invasion affects ecosystem functioning. However, we used an existing gradient in invader cover, which means we cannot rule out the possibility that some of our effects are caused by co-varying environmental factors. We corrected for environmental parameters such as soil pH, texture and elevation, and additionally tested for disturbance effects, however unmeasured factors could also have been important. It should also be noted that our findings are from (moderately) disturbed systems and *Prosopis* effects might be different in undisturbed areas. Experiments would be necessary to fully identify causal effects of *Prosopis* on function and whether *Prosopis* is indeed a driver; however, these are unlikely to be feasible or ethical. In addition, we were not able to sample all functions on all plots and low sample sizes might have obscured relationships for some functions. This underlines the importance of high sample sizes to uncover the complex effects of invaders on ecosystem functioning.

4.3 | Management implications

Many invasive trees, including *Prosopis* (Pasiecznik, Felker, Cruz, & Cadoret, 2001), were originally introduced to increase soil stability, carbon storage and soil fertility (Richardson & Rejmánek, 2011). We only found a positive effect of *Prosopis* on soil stability in Ethiopia, which was partly offset by the negative effects of losing herbaceous biomass. *Prosopis* also indirectly decreased soil fertility and SOC in both regions. This shows that *Prosopis* is not providing the anticipated benefits, mostly because it reduces native herbaceous species, which increase soil carbon stocks (Jackson et al., 2002) and are resilient against erosion (Bird, Herrick, Wander, & Murray, 2007). In the case of *Prosopis*, the failure to take into account the positive effects of the original vegetation has led to decreases in ecosystem functions that *Prosopis* was supposed to improve.

4.4 | Conclusions

Our study highlights the importance of indirect effects in explaining the impact of global change on ecosystem functioning. These results add to the evidence that biodiversity loss affects ecosystem functioning in real-world ecosystems (e.g. Delgado-Baquerizo et al., 2015; Soliveres et al., 2016), and that diversity loss is a major component of global change effects (Allan et al., 2015), by extending them to different contexts and global change drivers. However, they also indicate the importance of considering a wider range of indirect effects. Our study adds to the increasing evidence that biodiversity plays a key role in mediating global change effects on ecosystem functioning and highlights the necessity of reversing biodiversity loss in order to reverse environmental degradation.

ACKNOWLEDGEMENTS

This work was supported by the Swiss Programme for Research on Global Issues for Development (r4d), funded by the Swiss National Science Foundation and the Swiss Agency for Development and Cooperation, through the project 'Woody invasive alien species in East Africa: Assessing and mitigating their negative impact on ecosystem services and rural livelihood' (Grant Number: 400440_152085). T.E.W.L., U.S. and R.E. were supported by CABI with core financial support from its member countries (see <http://www.cabi.org/about-cabi/who-we-work-with/key-donors/>).

AUTHORS' CONTRIBUTION

T.E.W.L., U.S., R.E., S.K.C., L.N. and E.A. designed the experiment, T.E.W.L., A.A., P.R.M. and H.S. collected the data, L.N. & S.K.C. provided logistical support in the field, T.E.W.L. performed the statistical analysis and wrote the first draft and all authors contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pv5kh6p> (Linders et al., 2019)

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Linders TEW, Schaffner U, Eschen R, et al. Direct and indirect effects of invasive species: Biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. *J Ecol.* 2019;107:2660–2672. <https://doi.org/10.1111/1365-2745.13268>